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bilateral suction ablation of either the entire auditory cortex, or more localized cortical regions. This research revealed that these behavioral adjustments are predominantly under sub-cortical control, but that the DSCF area of the auditory cortex plays an important role in the 'fine-tuning' of the emitted pulse frequency. Second, we examined the role of the auditory cortex in the perception of biosonar signals. This was accomplished by conditioning the bats to discriminate between biosonar signals that varied along some stimulus parameter (e.g., echo delay) using a leg flexion shock avoidance procedure. We then created 'reversible ablations' by application of muscimol to selected areas of the auditory cortex. Muscimol is an agonist of the inhibitory neurotransmitter γ -aminobutyric acid (GABA). These studies revealed that discrete functional areas within the auditory cortex mediate perception of particular parameters of the biosonar signal (e.g., echo Doppler shift or echo delay). Overall, this research demonstrates the linkage between the electrophysiologically defined cortical maps in the auditory cortex and biosonar behavior.

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REPORT OF INVENTIONS AND SUBCONTRACTS

(Pursuant to "Patent Rights" Contract Clause) (See Instructions on Reverse)

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FINAL REPORT

The major aim of this project was to examine, by means of critical lesion experiments, whether the functional organization of the mustached bat's, *Pteronotus parnellii parnellii*, auditory cortex is related to biosonar behavior in the manner inferred from previous neurophysiological experiments. For approximately half of the 3-year grant period, we focused on natural biosonar behaviors elicited by swinging a bat on a pendulum towards a large target. First, we quantitatively analyzed the behavioral adjustments the bat makes in the frequency, intensity, duration, and rate of emission of its biosonar pulses during target-directed 'flight'. Next, we examined changes in these behavioral adjustments following bilateral ablation of either the entire auditory cortex, or more localized cortical regions.

For the second half of the grant period we focused on the role of the auditory cortex in the perception of biosonar signals. This was accomplished by conditioning the bats to discriminate between biosonar signals that varied along some stimulus parameter (e.g., echo delay) using a leg flexion shock avoidance procedure. We then created 'reversible ablations' by application of muscimol to selected areas of the auditory cortex. Muscimol is an agonist of the inhibitory neurotransmitter γ -aminobutyric acid (GABA).

The major results of each of these lines of research are described below.

I. PENDULUM EXPERIMENTS: BEHAVIORAL ADJUSTMENTS OF THE BIOSONAR SIGNAL DURING FLIGHT.

A. Behavior of Normal (Unablated) Bats.

The biosonar signal (pulse) of the mustached bat has four harmonics (H_{1-4}), each consisting of a long constant frequency component (CF_{1-4}) followed by a short frequency modulated

component (FM_{1-4}). As the bat approaches a target it systematically modifies its pulses to optimize the extraction of information from the echoes. These behavioral responses include: (i) Doppler-shift (DS) compensation in which the bat adjusts the frequency of its pulses to correct for the DS in the echoes. This maintains the echo CF_2 at a frequency to which the bat's cochlea is very sharply tuned, slightly above the CF_2 frequency of the bat's pulses when it is at rest ($F_{rest} \sim 61$ kHz). (ii) Echo intensity compensation, in which the bat lowers its pulse intensity as it approaches a large target, thus maintaining the echo intensity within a suitable range for auditory processing. (iii) and (iv) Duration and rate adjustments, in which the bat first increases its pulse duration to facilitate target identification, then shortens its pulse duration while increasing its pulse rate to facilitate target analysis.

We examined these responses, especially DS compensation, by swinging bats on a pendulum towards a large target over a distance of 3.6 m. Eight bats were given 15 - 30 swings per day for 6 - 25 days. (i) On 97% of all swings the bats showed strong DS compensation as the pendulum approached the target. They did not show DS compensation on the backswing. (ii) On 40-50% of all swings, the bats clearly displayed the other responses. The bats typically increased their pulse intensity a small amount early in the pendulum swing, then decreased pulse intensity by as much as 18 dB as the target was more closely approached. They increased their pulse intensity during the backswing. (iii) Pulse duration increased from about 20 ms to 23 ms early in the forward swing, decreased to about 18 ms as the target was more closely approached, and then increased to 20 ms by the end of the backswing. (iv) The instantaneous repetition rate increased from about 17 pulses/s at the start of the forward swing to about 28 pulses/s near the target, then decreased to about 10 pulses/s by the end of the backswing. Pulses usually occurred in trains of 1-2 pulses, with longer trains occasionally occurring near the target.

The maximum DS on the pendulum was 1.34 kHz, and the maximum DS compensation was $146 \text{ Hz} \pm 98 \text{ Hz S.D.}$ less than this value. There was a reaction time of $104 \text{ ms} \pm 36 \text{ ms}$ between the

maximum echo DS and the maximum compensation. Scatter plots of the bats' pulse CF₂ frequencies against the echo DS revealed a difference in the pattern of DS compensation for the acceleration and deceleration phases of the pendulum forward swing. When we corrected for the reaction time, however, the data points for the acceleration and deceleration phases were superimposed. Linear regressions on these plots revealed that the bats were compensating for an average of 80% of the echo DS. The bats were more consistent in DS compensation across swings during pendulum deceleration than acceleration, suggesting that they were attending more closely to the target during deceleration.

It was also possible to correct for the reaction time by plotting the bat's CF₂ frequency on pulse(n) against the DS in echo(n-1), echo(n-2), or echo(n-3). These results suggest that the bats were compensating in a non-predictive fashion to the Doppler shift in previous echoes. Such non-predictive tracking may be a general feature of the behavioral adjustments made by bats while echolocating.

The F_{rest} of four of the eight bats significantly declined by as much as 366 Hz during the 10 - 61 days of the experiment, averaging 3 - 5 Hz/day for three of the bats, and 29 Hz/day for the fourth. Also, the F_{rest} measured immediately after each test session was significantly lower than the pretest F_{rest} by an average of 121 ± 79 Hz.

Occasionally, a bat would not vocalize until part way through the forward swing, but then its first pulse would be at the frequency appropriate to compensate for the echo DS. This implies memory for the amount of DS occurring at various points along the pendulum arc.

B. Behavior of Bats Following Cortical Ablations.

We examined the effect of subpial suction ablations of different parts of the cortex on these behavioral responses, especially DS compensation. (i) The Doppler-shifted CF (DSCF) processing area of the auditory cortex (AC) was bilaterally ablated

in two bats. This area only represents frequencies in the range of Doppler-shifted echo CF₂'s (~ 60.6 kHz to 62.3 kHz) and thus has been hypothesized to be important for DS compensation. (ii) The cingulate cortex (Cng) was bilaterally ablated in two bats. The anterior part of the Cng contains a motor map of the pulse CF₂ frequencies emitted during DS compensation. (iii) Three bats received large bilateral ablations of the AC, as did one of the bats that had previously had its Cng ablated.

Following the bilateral ablations of the DSCF area, the maximum DS compensation averaged only 54% of the maximum DS (622 Hz less than complete compensation), and the acceleration reaction time doubled (from 101 ms to 194 ms). In contrast, the deceleration reaction time decreased slightly (from 128 ms to 108 ms). When the consistency of DS compensation was measured across swings within each session, these bats showed a 59% increase in variability following the DSCF area ablations (S.D. of pulse CF₂ frequency at the point of maximum DS compensation = 197 Hz).

Three of the four AC-ablated bats (including the bat with the prior Cng ablation) showed a pattern of results similar to the DSCF area-ablated bats, but more severe. These three bats compensated for an average of only 30% of the maximum DS. They showed a 92% increase in the variability of their DS compensation measured across swings within each session. In only one of these bats, J07-15, was it possible to make reliable measurements of reaction times. This bat showed a 254% increase in its acceleration reaction time (from 84 ms to 283 ms) and a 128% increase in its deceleration reaction time (from 94 ms to 214 ms).

The final AC-ablated bat, J12-21, showed a gradual increase in its F_{rest} of up to 4 kHz over repeated swings on the pendulum. Its F_{rest} returned to normal within 15 minutes of the last swing in a session. This effect occurred on each test session until the animal died. The increase in F_{rest} within a test session resulted in extreme variability in its DS compensation across swings. Within individual swings the bat showed a relatively normal pattern of change in pulse CF₂ frequencies as a function of echo Doppler shift, except that all the CF₂ frequencies were shifted upwards, often above the pretest

F_{rest} . Since DS compensation is measured relative to the pretest F_{rest} , this bat showed negative compensation. Another of the AC-ablated bats, J10-05, showed a similar effect that disappeared after one week post-ablation.

Following bilateral ablation of the Cng no significant deficits were observed in DS compensation. The two bats compensated for 88% of the maximum DS (vs 89% for normals), and showed a small (18%) decrease in the variability of their DS compensation across swings within a test session. Their acceleration and deceleration reaction times each increased by a small statistically nonsignificant amount (acceleration from 102 ms to 122 ms, and deceleration from 148 ms to 164 ms).

With respect to the other behavioral responses, only two clear patterns emerged. The percentage of swings on which amplitude compensation occurred significantly decreased in 3/4 AC-ablated bats, and the percentage of swings on which pulse duration was adjusted as a function of target distance significantly decreased in 4/4 AC-ablated bats.

II. CONDITIONED SHOCK AVOIDANCE TASK: PERCEPTION OF BIOSONAR SIGNALS.

A. Perception of Echo Doppler Shift (Frequency Discrimination).

As previously mentioned, during flight the mustached bat adjusts the frequency of its pulse so as to maintain the CF_2 of the Doppler-shifted echo at a constant frequency to which its cochlea is very sharply tuned. This Doppler shift (DS) compensation likely is mediated by the Doppler-shifted CF (DSCF) processing area of the primary auditory cortex which only represents frequencies in the range of Doppler-shifted echo CF_2 's (~ 60.6 kHz to 62.3 kHz).

We examined this hypothesized role of the DSCF area by training four bats to discriminate between different trains of artificial pulse CF_2 - echo CF_2 pairs (tone bursts). A discriminated

shock avoidance procedure was employed, using a leg flexion response. For one stimulus, the S+, the pulse and echo CF₂'s were the same frequency ($\Delta f = 0$). A leg flexion during the S+ turned off both the S+ and the scheduled shock. For a second stimulus, the S-, the echo CF₂ was 0.05, 0.1, 0.3, 0.5, or 2.0 kHz higher than the pulse CF₂. No shock followed the S-, and leg flexions had no consequences. Correct responses consisted of a leg flexion during the S+ and no flexion during the S-. When a bat correctly responded at better than 75% for all the Δf 's, muscimol, a potent agonist of gamma-aminobutyric acid (GABA), was bilaterally applied to the DSCF area to create a 'reversible' ablation. Performance on each Δf discrimination was then measured.

Initial attempts to condition the bats to flex their legs to our tone burst pulses and echoes failed. When broad-band noise bursts were substituted, however, the response was rapidly conditioned. The noise band-width was gradually reduced, and then replaced with the tone bursts. Discrimination training, described above in 2., then commenced. Throughout this procedure, the bats maintained their responding to the stimuli. This pattern of results may be related to Seligman's (1970) concept of 'preparedness': animals are biologically prepared to form an association between certain types of stimuli but not others.

After the application of muscimol to the DSCF area, performance on the Δf discriminations clustered into three categories: fine ($\Delta f = 0.05$ and 0.1 kHz), intermediate ($\Delta f = 0.3$ and 0.5 kHz), and coarse ($\Delta f = 2.0$ kHz). Muscimol disrupted performance on the fine and intermediate frequency discriminations for approximately 2-3 h, and 6-7 h, respectively. Performance on the coarse discrimination was unaffected.

Three statistical analyses were performed on the percentage of correct responses during time windows immediately prior to muscimol application and 0.2 - 1.7 h, 1.7-3.2 h, and 24 - 25.5 h post-muscimol. (i) Comparison of performance before (baseline) vs. after muscimol application allowed us to determine whether significant deficits in performance had occurred and how long these deficits lasted. Performance on the fine discriminations was

significantly disrupted for the first two post-muscimol time windows, performance on the intermediate discriminations was significantly disrupted only for the first of these windows, and performance on the coarse discrimination was never significantly disrupted. (ii) Comparison of performance relative to chance (50%) allowed us to determine whether there was any retention of the learning. The bats always performed above chance on the coarse discrimination, and performed above chance during all but the first post-muscimol time window on the intermediate discriminations. On the fine discriminations they failed to perform above chance for the first two post-muscimol time windows. (iii) Comparison of the Δf discriminations within each time window allowed us to determine directly whether muscimol differentially affected these discriminations. Between 0.2 - 1.7 h post-muscimol, performance on the coarse discrimination was significantly worse than performance on the fine or intermediate discriminations. Between 1.7 - 3.2 h post-muscimol, performance on coarse and intermediate discriminations differed from performance on the fine discriminations. By the final time window, 24 - 25.5 h post-muscimol, there were no significant differences among the different discriminations.

Previous studies had suggested that following AC ablations animals tested with discriminated shock avoidance tasks have difficulty withholding responses on S- trials. When we examined the S+ and S- errors before and after the ablation for each bat, however, no consistent pattern emerged.

Application of muscimol to the FM-FM area of the auditory cortex, an area unrelated to the analysis of echo Doppler shifts, had no effect on any of the frequency discriminations. This demonstrates that the deficits observed when the DSCF area was ablated were not due to some general disruption of learning, motivation, etc.

These results demonstrate that reversible focal ablation of the DSCF area of the AC produces a temporary disruption in the ability of bats to detect small or moderate echo Doppler shifts. This is consistent with the hypothesis that the DSCF area is involved in DS compensation. They also provide the first clear evidence of a

significant deficit in frequency discrimination following a focal bilateral ablation in the primary auditory cortex. Finally, these results demonstrate the value of the reversible ablation technique for exploring the behavioral significance of computational maps in sensory cortex.

B. Perception of Echo Delay (Temporal Discrimination).

Neurons in the FM-FM area of the auditory cortex specifically respond to the combination of the FM sweep from the first harmonic of the emitted pulse (FM₁) and a higher harmonic of the echo (FM₂₋₄). They are tuned to particular echo delays. The best delay for these neurons systematically varies across the FM-FM area, suggesting that this area is important for processing echo delays, *i.e.*, target ranging.

The temporal discrimination task used trains of 24 pairs of PFM₁-EFM₂. For S+ trials the echo delay was always set at 4 ms (P onset to E onset). For S- trials, the echo delay for successive P-E pairs within the train was jittered between 4 ms and 4 ms + Δt , where $\Delta t = 1, 2, 4, 6, 16, \text{ or } 36$ ms. Both the PFM₁ and the EFM₂ were 3.5 ms long, with 0.5 ms rise and fall times and were repeated at 20 pairs/s. The PFM₁ linearly swept from 31 kHz to 21 kHz, and the EFM₂ linearly swept from 62 kHz to 46 kHz. The PFM₁ and the EFM₂ were delivered at 80 and 75 dB SPL, respectively. For the 36 ms Δt the presentation rate was decreased to 10 pairs/s.

When a bat correctly responded at better than 75% for all the Δt 's, muscimol was bilaterally applied to the FM-FM area. Performance on each Δt discrimination was then measured. Application of muscimol to the FM-FM area disrupted temporal discriminations, but its effect varied as a function of the Δt employed. From the bats' performance, the temporal discriminations could be divided into three clusters: coarse ($\Delta t = 36$ ms), intermediate ($\Delta t = 4, 6, \text{ or } 16$ ms), and fine ($\Delta t = 1 \text{ or } 2$ ms). The coarse discrimination suffered no significant disruption. Shortly after muscimol application (0.2 to 2.2 hours), performance on both

the intermediate and fine discriminations was significantly disrupted. At 2.2 to 4.2 hours after muscimol application, performance was still significantly disrupted on the fine discriminations, but not the intermediate discriminations. Performance on the former returned to normal by 7 to 8 hours after muscimol. Application of muscimol to the DSCF area had no significant effect on any of the temporal discriminations

These results indicate that the FM-FM area is important for fine temporal discriminations involving echo delays. The limits of the temporal discrimination deficits are predictable from the electrophysiologically determined range of echo delays mapped in the FM-FM area.

PUBLICATIONS RESULTING FROM GRANT

Original articles

1. Gaioni, S.J., Riquimaroux, H., & Suga, N. Biosonar behavior of mustached bats swung on a pendulum: *Journal of Neurophysiology*, in press.
2. Riquimaroux, H., Gaioni, S.J., & Suga, N. Cortical computational maps control auditory perception. (Order of first two authors determined by lot.) *Science*, in press.
3. Riquimaroux, H., Gaioni, S.J., & Suga, N. Inactivation of the Doppler-Shifted Constant Frequency Area of the auditory cortex with muscimol impairs frequency discrimination by the mustached bat. Submitted to *Journal of Neurophysiology*.
4. Gaioni, S.J., Riquimaroux, H., & Suga, N. Biosonar behavior of mustached bats swung on a pendulum following ablation of the auditory and cingulate cortices. In preparation.

5. Riquimaroux, H., Gaioni, S.J., & Suga, N. Inactivation of the FM-FM Area of the auditory cortex with muscimol impairs temporal discrimination by the mustached bat. In preparation.

Review articles

1. Suga, N. Biosonar and neural computation in bats. *Sci. Am.* **262** (6): 60-68, 1990.
2. Suga, N., Olsen, J.F., and Butman, J.A. Specialized subsystems for processing biologically important complex sounds: Cross-correlation analysis for ranging in the bat's brain. In: *The brain*. Cold Spring Harbour Quant. Biol., in press.

Abstracts

1. Gaioni, S.J., Riquimaroux, H., & Suga, N. Effects of bilateral ablations of the auditory cortex and/or cingulate cortex on the biosonar behavior of the mustached bat. *Soc. for Neurosci. Abstr.* **14** (2): 1100, 1988.
2. Riquimaroux, H., Gaioni, S.J., & Suga, N. Effects of bilateral ablation of auditory and/or cingulate cortices on bat echolocation behavior. *Abstracts of the Twelfth Midwinter Research Meeting of the Association for Research in Otolaryngology*: 28, 1989.
3. Riquimaroux, H., Gaioni, S.J., & Suga, N. Muscimol application to the bat's auditory cortex disrupts fine frequency discrimination of biosonar signals. *Soc. for Neurosci. Abstr.* **15** (2): 1292, 1989.
4. Riquimaroux, H., Gaioni, S.J., & Suga, N. Functional involvement of auditory cortex in fine frequency discrimination of biosonar signals in the bat. *J. Acoust. Soc. of Am.* **86** Suppl. 1: S99, 1989.

5. Riquimaroux, H., Gaioni, S.J., & Suga, N. Muscimol disrupts temporal discrimination by the FM-FM area of the mustached bat's auditory cortex. *Soc. for Neurosci. Abstr.* 16: accepted.

N.B. Reprints of articles will be sent as soon as they become available.

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